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Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients

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Summary

1. Plant interactions play a central role in regulating plant communities and this role can be altered by abiotic stress. With increasing stress, ecological theory predicts that the role of competition decreases whilst that of facilitation increases. Such predictions have been tested with short-term plant removal experiments using two distinct indices evaluating the role of plant interactions: the intensity (absolute impact) and the importance (impact relative to that of other abiotic constraints) of plant interactions.

2. Using data on individual tree radial growth from more than 17 000 forest plots covering the habitat conditions of 16 species in the Alps and the Jura mountains of France, we show that non-manipulative estimates of plant interactions provide an alternative to this experimental approach. We developed a Bayesian neighbourhood growth competition model to test theoretical predictions about plant–plant interactions with a much larger spatio-temporal scope and set of study species than classically used in experimental studies of plant–plant interactions.

3. Our analyses revealed that competition – measured as neighbours effects on adult tree growth – varies in importance but not in intensity along two major bioclimatic gradients (degree-day sum and water availability). Observed patterns of competition importance differed between shade-tolerant and shade-intolerant tree species. First, the mean importance of competition was found to be much higher for shade-intolerant species. Second, for shade-intolerant species the importance of competition remained high even at low crowding indices (i.e. at a low competitor density), whereas for shade-tolerant species competition only became important at high crowding indices.

4. *Synthesis*. Our non-manipulative approach to the study of plant–plant interactions allows analysing interactions among many species over large climatic gradients. Our results clearly demonstrate that a quantitative estimation of density dependence effects is key to understanding how plant–plant interactions vary along abiotic gradients. Growth predictions derived from our model can easily be integrated with other results on tree regeneration and mortality in individual-based models to investigate how plant–plant interactions drive tree population and community dynamics under varying climatic conditions.

Key-words: competition importance and intensity, environmental gradients, plant–plant interactions, stress gradient hypothesis, tree radial growth

Introduction

Negative and positive plant–plant interactions play a central role in regulating the composition and dynamics of plant communities (Keddy 1989; Brooker *et al.* 2008). The structuring influences of these interactions can be altered by external drivers such as climatic conditions or nutrient availability and are key to forecasting the impacts of climate change on plant communities (Brooker 2006). Debates have raged for decades over how the structuring influences of plant–plant interactions

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vary along abiotic stress gradients (Grime 1979; Tilman 1988; Keddy 1989; Brooker *et al.* 2008; Maestre *et al.* 2009). Recently this debate has been focused on the stress gradient hypothesis (SGH), which predicts that the role of competition decreases and facilitation increases with increasing stress, although we note that the role of facilitation may diminish in very severe conditions (Brooker *et al.* 2008; Maestre *et al.* 2009). Numerous short-term removal experiments have led to results either supporting or rejecting the SGH (see Goldberg *et al.* 1999; Maestre, Valladares & Reynolds 2005 and Lortie & Callaway 2006 for meta-analyses). A criticism of these experiments is that they are usually limited to few species, growing under a limited set of environments (typically low vs. high stress levels), for a short period (typically a few months) and with a poor description of the underlying abiotic environment (Brooker *et al.* 2008; Maestre *et al.* 2009). In long-lived plant communities, such as forests, the effects of competition may take many years to materialize and are likely to vary with the species' ecological strategies, i.e. stress tolerator vs. competitor (Brooker *et al.* 2008; Maestre *et al.* 2009). Measurements taken from forest inventory plots provide an alternative to the experimental approach, offering the opportunity to test plant–plant interaction theories over large spatial and temporal scales and with large numbers of tree species with different ecological strategies.

There is also the difficulty of evaluating how plant–plant interactions influence the structure of plant communities (Goldberg *et al.* 1999; Brooker *et al.* 2005; Brooker & Kikvidze 2008; Freckleton, Watkinson & Rees 2009; Gross *et al.* 2009). A study of plant growth may demonstrate that species compete strongly for resources when grown closely together (i.e. that competition is intense), but this observation does not necessarily imply that growth is mostly limited by competition; it could be that abiotic stress is a more limiting factor. This distinction is important because short-term removal experiments have shown that indices of intensity (the absolute impact) and indices of importance (the impact relative to that of other constraints) of plant–plant interactions may vary in distinct ways along environmental gradients (Brooker *et al.* 2005; Brooker & Kikvidze 2008). Studies using indices of importance remain rare (Kikvidze & Brooker 2010). In addition, it is unclear how the effects of competition on individual plant performance (i.e. growth or mortality) affect the structure and composition of plant communities (Lamb & Cahill 2008; Freckleton, Watkinson & Rees 2009; Mitchell, Cahill & Hik 2009): this can only be fully understood when the effects of plant–plant interactions on all phases of the life cycle are integrated using quantitative models that explicitly account for the density dependence of competition (Freckleton, Watkinson & Rees 2009). Recent advances in statistical methods enable researchers to investigate this issue by using natural variation in neighbourhood density to quantify competitive effects on tree radial growth (Canham *et al.* 2006). These non-manipulative estimations of tree–tree interactions are particularly promising because they include the density dependence effect of competition. This represents a major advance which bridges the gap between empirical data and models, providing a tool for progressing our understanding of community dynamics.

Here we use neighbourhood models to analyse how the effects of tree–tree interaction on adult growth vary across large spatial scales which encompass strong environmental gradients and shifts in species composition. French National Forest Inventory (FNFI) data from more than 17 000 plots in the French Alps and Jura mountains were used to estimate competitive effects based on responses to variation in the local density for 16 species. Using hierarchical Bayesian methods we developed species–specific radial-growth models including effect of tree size, a 'crowding' index of local tree–tree interaction, and the effect of two major abiotic drivers of tree growth, namely degree-day sum (Loehle 1998; Rickebusch *et al.* 2007) and water availability (Pederson *et al.* 2006; Littell, Peterson & Tjoelker 2008). Comparison of tree radial growth models enabled us to test whether increasing abiotic stress leads to (i) lower competition intensity and a shift to facilitation, and (ii) lower competition importance, and whether these effects vary along an ecologically important axis for tree species: the axis of shade tolerance.

Materials and methods

FORESTRY INVENTORY DATA SET

The FNFI comprises a network of temporary plots established on a grid of *c.* 500 × 500 m. If a particular grid node falls within a forested area, a plot is established, the soil type is characterized and the growth of trees determined by dendrometry. We focus on a 66 000-km^2 study area that extends from the Jura Mountains to the south of the Alps (Fig. 1), within which the climate of the lowlands varies from Mediterranean through oceanic to continental. The mean annual temperature over the period 1980–2000 ranges from 3.5 to 15.7 °C and the mean annual precipitation from 480 to 2220 mm year^{-1}. Data were collected over 10 years, with the timing varying between administrative regions (see Table S1 in Supporting Information). Measurements were taken in three concentric circular plots of different radii, based on diameter at breast height (d.b.h.). All trees with d.b.h. > 7.5 cm, > 22.5 cm and > 37.5 cm were measured within a radius of 6 m, 9 m and 15 m, respectively. For each measured tree, stem diameter, species, status (dead or alive), and radial growth over 5 years were recorded. The radial growth was determined from two short cores taken at breast height. Soil properties were analysed using a soil pit of up to 1 m depth located in the centre of the plot. One or two soil horizons were distinguished from the soil pit, and depth, texture (based on eight classes using the soil texture triangle of Jamagne (1967)) and coarse fragment content were recorded for each horizon. Maximum soil water content was computed based on these three variables, using standard values of water retention for each texture class (Baize & Jabiol 1995).

We selected 16 common tree species for analysis (Table 1) after excluding exotic species, species with fewer than 250 live individuals and sub-canopy trees. In addition, if only the genus of some species had been recorded, such groups were discarded if the constituent species had markedly different ecological strategies (i.e. the group with *Acer campestre*, *Acer opalus* and *Acer monspessulanum*). We also excluded plots if any evidence of a recent (< 5 years) logging operation or disturbance such as fire or wind-throw was recorded during the inventory.

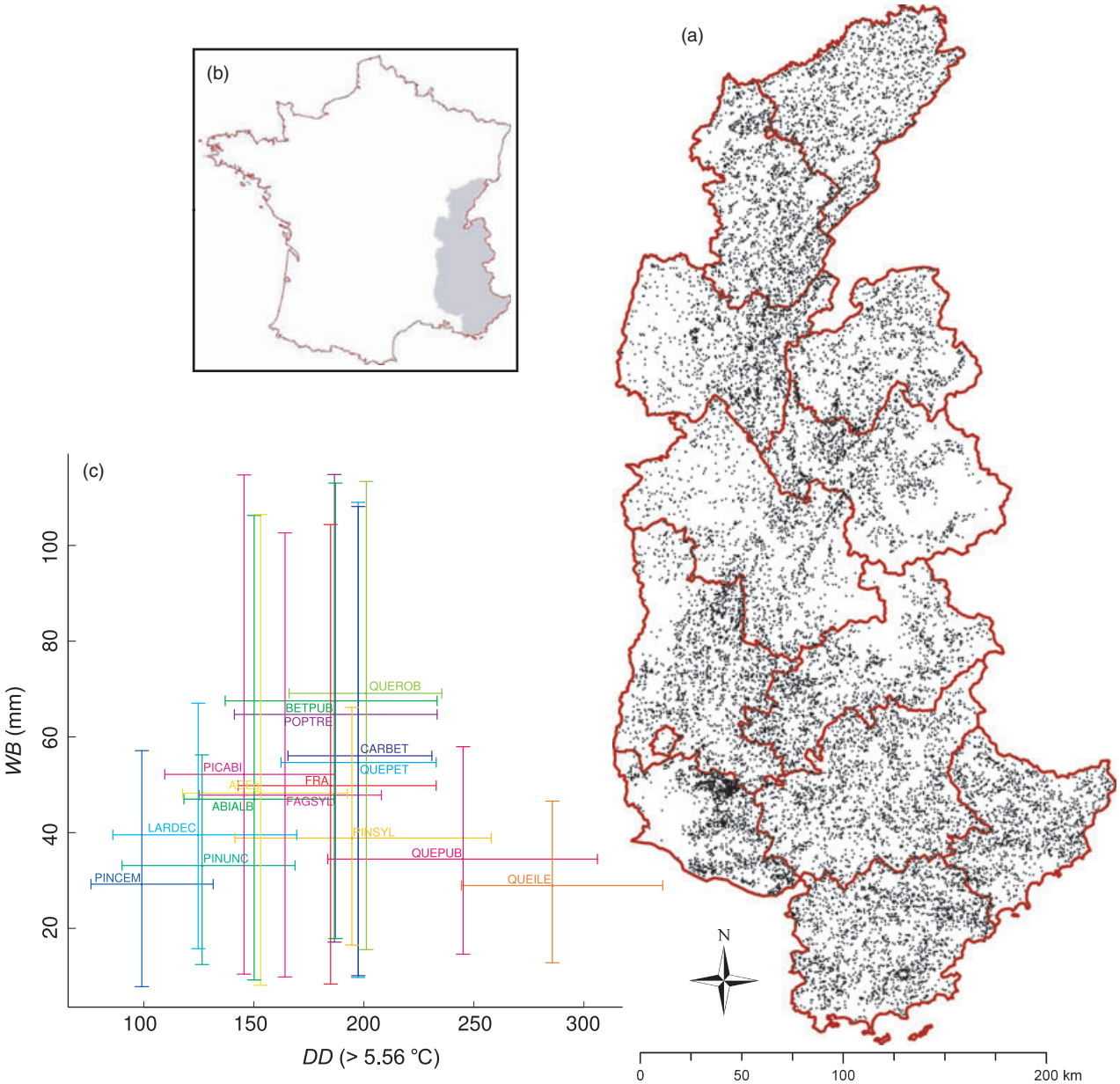

Fig. 1. Map of the location of all French National Forest Inventory (FNFI) plots over the study area, showing limits of the 12 administrative regions (a). The location of the study area within France (b). The position of the species in the climatic space based on the mean and 95% confidence intervals of the degree day (*DD*) and water budget (*WB*) conditions they experience (c). See Table 1 for species acronyms.

CLIMATIC VARIABLES

Our analysis required climatic data with high spatial resolution, because climate is extremely variable over small distances in mountainous areas. We also needed yearly climatic data because different administrative regions had scheduled data collection for different years, so growth data corresponded to different 5-year windows in different regions. We downscaled the climate data AURHELY of Météo France (1×1 km grid; Benichou & Le Breton 1987) to a 100×100 m grid using the moving-window regression method of Zimmermann *et al.* (2007) and a 50×50 m digital elevation model (DEM) from Institut Géographique National. We then generated the annual variability of monthly temperature and precipitation data by adding monthly anomalies derived from downscaled time series of the CRU TS 1.2 data set (Mitchell *et al.* 2003). Using the DEM we also computed mean monthly potential radiation with the Northern Hemisphere corrected method of Kumar, Skidmore & Knowles (1997).

Rather than exploring numerous climatic variables using a lengthy model selection procedure we selected two bioclimatic variables that are known to have strong impacts on tree growth: the degree-day sum over the growing season (*DD*) and water availability over the growing season (*WB*). Focusing on these variables helps forge links between our phenomenological approach, process-based models (particularly the model FORCLIM, Bugmann (1996)) and the ecophysiological literature. We calculated *DD* as the sum of daily temperature for days with average temperature > 5.56 °C over each month of the growing season (defined as the months with an average temperature

Table 1. List of tree species (or groups of species) and their acronyms. For each species are listed: number of individuals, number of plots, average 5-year radial growth, average tree diameter and height (with 95% confidence intervals) and shade tolerance index of Niinemets & Valladares (2006) (with standard error when available)

Acronyms	Species or group of species	N° of trees	N° of plots	Average 5-years radial growth (cm)	Average diameter (cm)	Average height (m)	Shade tolerance index
ABIALB	*Abies alba*	12885	2110	1.11	32.96 (8.27–69.07)	18.9 (5.5–34)	4.6 (0.06)
FAGSYL	*Fagus sylvatica*	21291	3275	0.6	22.07 (7.95–55.7)	15.54 (6.5–29.5)	4.56 (0.11)
PICABI	*Picea abies*	19651	2710	1.09	31.32 (8.59–65.25)	19.44 (6–34.5)	4.45 (0.55)
PINSYL	*Pinus sylvestris*	21962	3186	0.57	22.32 (8.27–46.79)	10.01 (4.09–19.5)	1.67 (0.33)
LARDEC	*Larix decidua*	6557	1000	0.68	32.25 (8.91–62.38)	17.55 (5.8–29.6)	1.46 (0.29)
QUEPET	*Quercus petraea*	7325	1441	0.61	24.98 (8.27–59.84)	15.43 (6.19–26.6)	2.73 (0.27)
QUEPUB	*Quercus pubescens*	22023	3268	0.36	14.09 (7.95–35.33)	7.79 (3.9–14.74)	2.31 (0.22)
QUEROB	*Quercus robur*	2235	669	0.83	33.84 (8.91–67.48)	18.25 (7.9–27.5)	2.45 (0.28)
QUEILE	*Quercus ilex*	9699	1298	0.26	10.8 (7.95–19.09)	5.73 (3.4–9.5)	3.02 (0.19)
PINCEM	*Pinus cembra*	271	85	0.49	34.63 (8.91–71.46)	13.25 (4.92–20.52)	2.87 (0.3)
PINUNC	*Pinus uncinata*	2230	325	0.44	20.47 (8.27–42.65)	10.11 (4.09–18)	1.2 ()
POPTRE	*Populus tremula*	1610	460	0.94	18.15 (7.95–43.21)	15.1 (7.5–25)	2.22 (0.07)
ACEg	*Acer pseudoplatanus* & *Acer platanoides*	2501	993	0.78	20.46 (7.95–48.7)	15.21 (7.3–25.6)	3.97 (0.11)
BETPUB	*Betula pubescens*	1030	423	0.77	19.81 (8.27–44.96)	15.55 (7.34–25.6)	1.85 (0.07)
CARBET	*Carpinus betulus*	7811	1403	0.51	13.46 (7.95–32.14)	13.06 (7.5–20.79)	3.97 (0.12)
FRA	*Fraxinus excelsior*. *Fraxinus oxyphylla* & *Fraxinus ornus*	5104	1536	0.86	19.73 (7.95–48.7)	16.55 (8.5–27.2)	2.84 (0.20)

> 5.56 °C). It was computed across the study area using the interpolation method described in Zimmermann & Kienast (1999). We computed the average *DD* for the 5 years corresponding to each radial growth measurement. We calculated *WB* from monthly averages of temperature, precipitation and potential radiation, as well as soil properties, using a 'bucket approach' (Bugmann & Cramer 1998; see Appendix S1 in Supporting Information). This involved computing the monthly soil water content (SWCm) for each plot over the period 1980–2001, and then taking *WB* as the average SWCm over all the months of the growing season within the 5 years corresponding to each radial growth measurement. Species distributions along the two abiotic gradients of *DD* and *WB* are represented in Fig. 1.

CROWDING INDEX

An index of crowding (*CI*) was calculated for each target tree. For each tree *i*, basal area (m^2 ha^{-1}) of neighbouring trees on the plot was computed (as $\sum_{j \neq i} \pi D_j^2/4$ divided by the area of the plot where *D* is d.b.h.). The index of crowding was then computed as the neighbourhood basal area divided by the highest neighbourhood basal area recorded on any of the plots in which the species was present (as Canham *et al.* 2006). Thus, *CI* varied between 0 (no crowding) and 1 (maximum crowding) for each species, helping in comparison between species.

HIERARCHICAL BAYESIAN MODELLING

The radial growth of individual trees was modelled as a nonlinear function of bioclimatic variables (*DD* and *WB*), local interactions with neighbouring trees (*CI*) and tree diameter (*D*) using a hierarchical Bayesian model (Gelman *et al.* 2004). Separate models were fitted for the 16 selected species. After exploring different forms of the equation for modelling the effects of abiotic variables and crowding on growth, we decided to use eqn 1 as our main model; radial growth of individual *i* on plot *p* was modelled as:

$$G_{pi} = \frac{\alpha_p \times D^{\beta 1} \times DD^{\beta 2} \times WB^{\beta 3}}{1 + (CI/\gamma)^{\delta}} \quad \text{eqn 1}$$

where α, β_1, β_2, β_3, γ and δ are parameters to be estimated (model M1).

The crowding response curve (CRC) $1/1 + (CI/\gamma)^{\delta}$ describes the effect of neighbouring trees on the growth of the target tree with a logistic function (see Gómez-Aparicio, Canham & Martin 2008). If δ is positive, the CRC represents a competitive effect and γ represents the value of *CI* at which growth is reduced by half (see Fig. S1 in Supporting Information). If δ is negative, the CRC represents a facilitative effect (see Fig. S1). A model lacking the crowding effect (i.e. $G_{pi} = \alpha_p \times D^{\beta 1} \times DD^{\beta 2} \times WB^{\beta 3}$; model M0) was fitted and compared with M1 to test whether *CI* was an important factor controlling tree growth. Then a series of alternative models were fitted to test the hypothesis that the shape of the CRCs changed with bioclimatic variables *DD* and *WB*. We started by fitting models in which δ was a linear function of *DD* ($\delta = \delta_0 + \delta_1 \times DD$; model M2), *WB* ($\delta = \delta_0 + \delta_1 \times WB$; model M3), and both bioclimatic variables ($\delta = \delta_0 + \delta_1 \times DD + \delta_2 \times WB$; model M4). These models allowed us to test whether the process of competition changed along bioclimatic gradients (i.e. more or less growth reduction for a given *CI*) and whether there was a shift from competition to facilitation (a shift of δ to negative values).

Observations of trees from the same plot *p* are not independent and the trees share common biotic and abiotic conditions unexplained by our two environmental variables (i.e. soil fertility and pathogen outbreaks). Therefore, we included this unexplained plot-level variability by modelling α_p as a random log-normal variable. The likelihood function for model M1 as well as a detailed description of our priors is given in Appendix S2. We used R.2.7.1 Software (R Development Core Team 2008) for data manipulation and JAGS 1.0.3 (Plummer 2003) for hierarchical Bayesian modelling (the *runjags* package was used to interface between R and JAGS). We checked for convergence with two Monte Carlo Markov Chains (MCMC) using the potential

scale reduction factor Rhat, setting our convergence threshold at Rhat < 1.1 as recommended by Gelman *et al.* (2004). We ran MCMC for 20 000 iterations with a 5000 burning period and a thinning of 20. The most parsimonious model for each species was selected using the deviance information criterion (DIC; Spiegelhalter *et al.* 2002). We evaluated the goodness-of-fit of the best model by computing the proportion of deviance explained (1- Deviance of the model/Deviance of model null), the concordance correlation (CC) and the coefficient of determination (R^2), as recommended by Huang, Meng & Yang (2009). To evaluate the percentage of variance explained by the *CI* (i.e. a partial R^2) we computed the increase in R^2 when a crowding effect was added to the model (i.e. M1 vs. M0).

Changes in competition intensity

Index of competition intensity. Change in the intensity of plant–plant interactions along abiotic gradients is usually analysed using the following index:

$$C_{\text{int}} = (G_{-N} - G_{+N})/max(G_{+N}, G_{-N}) \qquad \text{eqn 2}$$

where G_{+N} and G_{-N} are the growth of the target species in the presence ($+N$) and absence ($-N$) of neighbours (Brooker & Kikvidze 2008). This index has been used mainly in analyses of short-term removal experiments, but we adapted it for use with observational data by using our models to predict G_{+N} and G_{-N} for each point along bioclimatic gradients.

We computed G_{+N} and G_{-N} using growth predictions from our most parsimonious models. For each species we used the model to predict the growth rate of 'non-crowded' trees (i.e. G_{-N}) and crowded trees (G_{+N}) for all points along the bioclimatic gradients. To make these predictions, we used the average diameter of the species in the model and varied one of the abiotic gradients while keeping the other abiotic gradient fixed at its mean. In the case of non-crowded trees, *CI* was set at 0. In the case of crowded trees, we set *CI* as its average value at each point along the bioclimatic gradient to take into account the potential effect of these abiotic variables on the crowding condition. We estimated the average *CI* at each point along the bioclimatic gradients by fitting a smooth curve between *CI* and the bioclimatic variable (*DD* or *WB*) using generalized additive models (*gam* function in R, with four degrees of freedom). Finally we used these predictions of G_{+N} and G_{-N} to compute C_{int}.

Density dependence effect. This index contrasts the growth of trees experiencing average levels of competition with the growth of trees unfettered by competition, but to understand competitive interactions more completely it is important to analyse how growth varies with crowding (i.e. density dependence effect of competition). To analyse how the density dependence of competition intensity was affected by the abiotic gradients we directly represented the change of the CRCs between two different levels of stress (for *WB* or *DD*). Substitution of eqn 1 into eqn 2 yields the expression of the index of competition intensity as C_{int} = 1-CRC*(CI)* [with CRC*(CI)* the value taken by the CRC at a given level of crowding]. Thus, changes in the C_{int} are directly related to changes in CRC. To test if there were statistically significant variations in the index C_{int} or the CRC between low and high levels of stress, we ran Monte-Carlo simulations based on the posterior distributions of model parameters to compute C_{int} and CRC predictive posterior distributions (Gelman *et al.* 2004). We then computed the 95% credible interval of the predictive posterior distributions to estimate uncertainties associated with C_{int} and CRC.

Table 2. Model selection statistics (Deviance Information Criteria, DIC) for the five candidate models describing the tree radial growth as a function of tree diameter (*D*), water budget (*WB*), degree-day sum (*DD*) and crowding index (*CI*). Models were fitted by hierarchical Bayesian methods. The best-fitting model is highlighted in bold. Model 0 includes *D*, *WB* and *DD* effects but no *CI* effect. Model 1 includes *D*, *WB*, *DD* and *CI* effects. Model 2 includes a *DD* effect on the shape of the *CI* response, whereas model 3 includes a *WB* effect and model 4 both *WB* and *DD* effects. See text for more details on the models. Three measures of goodness-of-fit of the best model are reported: the percentage of deviance explained (% of Dev best model), the concordance correlation (CC best model), and the coefficient of determination (R^2 best model) (see Huang, Meng & Yang 2009). The increase of R^2 due the inclusion of the tree interaction in the model (inclusion of *CI* between Model 0 and Model 1) is given by the *CI* partial R^2. See Table 1 for species acronyms

Species Acronym	Models					% of Dev best model	CC best model*	R^2 best model	CI partial R^2
	Model 0	Model 1	Model 2	Model 3	Model 4				
ABIALB	25763.7	25665.8	**25663.5**	25664	25666.2	29.0	0.795	0.530	0.158
FAGSIL	37097.7	37010.1	36993.1	37010.4	**36990**	35.5	0.818	0.590	0.098
PICABI	34666	34600.3	34571.9	34596	**34561.7**	34.1	0.810	0.569	0.187
PINSYL	39137.4	**38927.9**	38934.7	38930.4	38928.9	28.4	0.770	0.482	0.124
LARDEC	11110.2	10994.1	**10922.3**	11036.9	11054.1	32.0	0.787	0.520	0.117
QUEPET	12596.9	12456	12453.1	**12430.2**	12473.6	34.8	0.811	0.567	0.070
QUEPUB	28917.3	28852.1	28840.8	**28838**	28842.2	39.3	0.796	0.533	0.061
QUEROB	4219.3	4108.9	**4089.8**	4141	4126.6	26.8	0.771	0.470	0.056
QUEILE	5980.4	**5958.9**	5977.9	5972.5	5977.5	72.8	0.884	0.733	0.013
PINCEM	530.8	**461.4**	493.3	516.3	511.1	24.7	0.737	0.400	0.134
PINUNC	4002	**3953.3**	3979.1	3975.4	3963	28.2	0.767	0.475	0.135
POPTRE	2476.1	**2400.4**	2425	2440.2	2444.4	42.4	0.845	0.607	0.089
ACEg	4239	4183.7	**4174.3**	4183.4	4175.5	39.3	0.851	0.583	0.116
BETPUB	1915	1880.5	1885	**1872.4**	1885.8	33.5	0.830	0.541	0.149
CARBET	12780.2	12696.1	12705.9	**12686**	12700.7	34.6	0.802	0.543	0.099
FRA	9376.6	**9265.9**	9292.2	9292.1	9298.3	35.0	0.832	0.583	0.087

*A value of CC = 1 corresponds to a perfect agreement and any CC < 0 indicates a lack of fit.

Changes in competition importance

Index of competition importance. The importance of competition is quantified as:

$$C_{\text{imp}} = (G_{-N} - G_{+N})/(MaxG_{-N} - min(G_{+N}, G_{-N})) \quad \text{eqn 3}$$

where $MaxG_{-N}$ is the maximum value of G_{-N} along the abiotic gradient analysed. C_{imp} 'expresses the impact of competition as a proportion of the total environment' (abiotic constraint and competition; Brooker *et al.* 2005) and follows the definition of Welden & Slauson (1986). We used the same method as for C_{int} (see above) to predict G_{+N} and G_{-N} for all points along the bioclimatic gradients (*DD* or *WB*). $MaxG_{-N}$ was set as the maximum value of G_{-N} predicted over all points of the bioclimatic gradients (*DD* or *WB*). Finally, as for C_{int}, we used these predictions of G_{+N}, G_{-N} and $MaxG_{-N}$ to compute C_{imp}.

Density dependence effect. To understand how density dependence (i.e. the level of crowding) affected the competition importance, we analysed how the importance of competition varies with the *CI* by computing C_{imp} for different levels of *CI* using eqn 3. We did so by simply representing how C_{imp} changes with *CI* at a high level of stress (either *DD* or *WB*). We used the same Monte-Carlo simulations method as used for competition intensity to compute the 95% credible interval of the predictive posterior distributions, providing us with estimate uncertainties associated with C_{imp}.

Results

For all species there was a positive effect of size, degree-day sum (*DD*) and water budget (*WB*) on growth, but a negative effect of local crowding (see Fig. S2 and parameters in Table S2). Plots (not shown) of predictions vs. observations indicated that the models made unbiased predictions. R^2 of the best-supported models varied among species, from 0.4 to 0.73 (see Table 2 for other goodness-of-fit measures). The inclusion

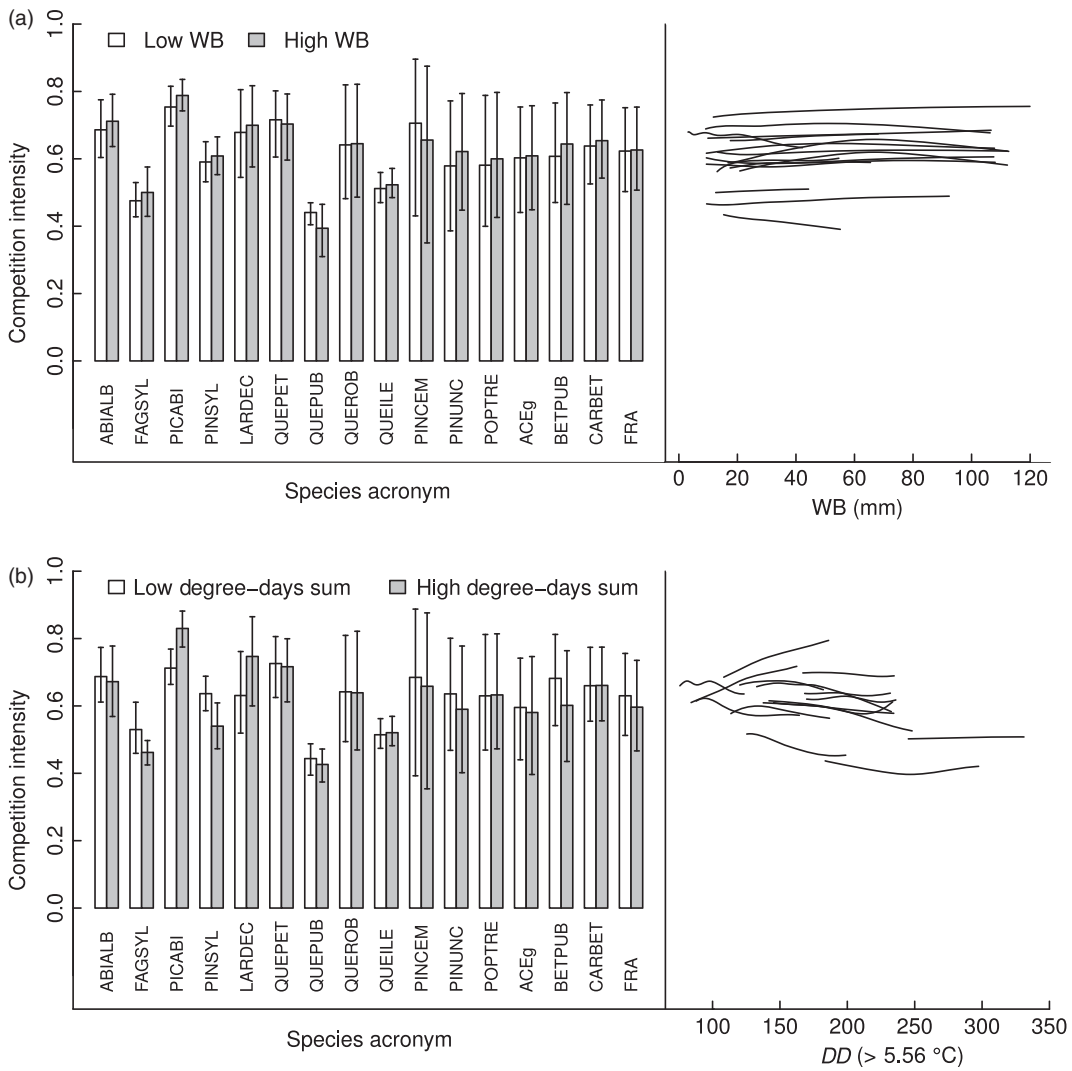

Fig. 2. Variation in competition intensity between low and high value of (a) water budget (*WB*) and (b) degree-day sum (*DD*). The biotic interaction intensity indices range from -1 (facilitation) to +1 (competition) and were computed at the 2.5% and at the 97.5% quantile of the abiotic condition experienced by the species (see text for more details). Non-overlapping 95% credible intervals (error bars) between high and low stress levels imply a statistically significant difference (at $P < 0.05$). The left panels represent the pattern of continues change of the index between high and low stress levels for the 16 species. See Table 1 for species acronyms.

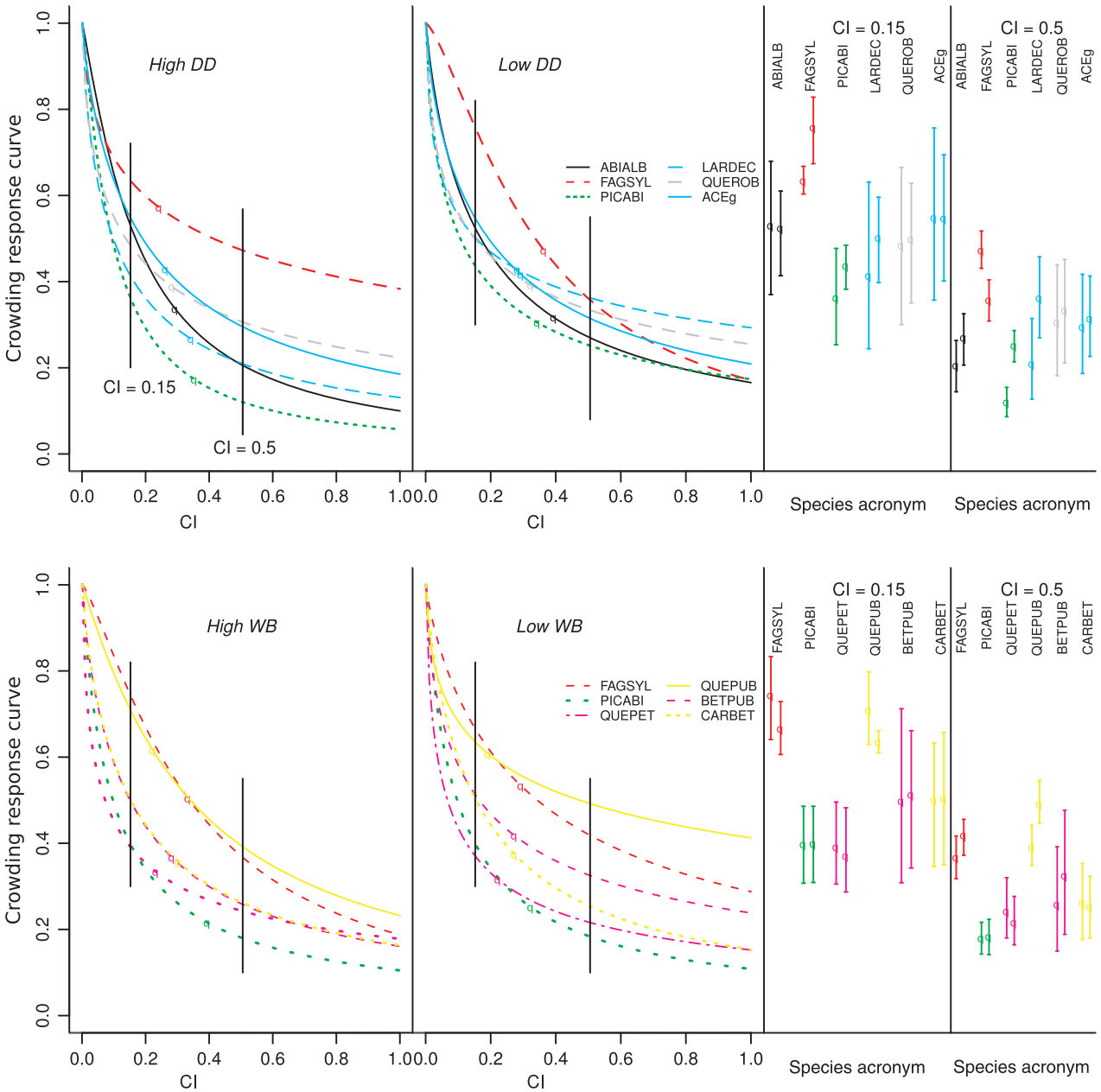

Fig. 3. Effect of degree-day sum (*DD*) (upper panel) and water budget (*WB*) (lower panel) on the shape of the crowding growth response curve. The crowding response curve (CRC) ranges between 0 and 1 and represents the proportion of growth reduction due to local crowding. The CRCs are represented at high and low levels of the abiotic variables (determined, respectively, as the 95% and 5% quantile of the abiotic condition experienced by the species). The point on the line represents the mean crowding index (*CI*) predicted by the gam model at low or high value of the abiotic factor. Only the species for which the best model includes an effect of the abiotic factor on the CRC are represented. The two right-hand panels represent the change in crowding response between low and high stress at $CI = 0.15$ or 0.5. Non-overlapping 95% credible intervals (error bars) of the CRC high and low stress levels imply a statistically significant difference (at $P < 0.05$). The vertical black lines in the left-hand panels are drawn to illustrate the position of $CI = 0.15$ and 0.5, from which the 95% credible intervals are derived. See Table 1 for species acronyms.

of the *CI* resulted in substantial increase in R^2 (an average increase of 10% among the 16 species; Table 2), confirming that local neighbourhood explain substantial proportion of the variation in individual tree growth.

COMPETITION INTENSITY

The shape of the CRC varied along bioclimatic gradients for 10 of the 16 species (Table 2). It was significantly influenced by water budget for four species, degree-days for four species, and by both variables for the remaining two species (models with lower DIC in Table 2). However, when indices of competition intensity were calculated from the model predictions, they showed rather little variation along these two bioclimatic gradients (Fig. 2); in fact the changes between low and high *WB* or *DD* were within the 95% credible intervals for all species except *Picea abies* (Fig. 2). The changes in mean *CI* with abiotic stress were

of small amplitude and resulted in small variation of the intensity of competition. There was no evidence of a shift to facilitation with increasing abiotic stress for any of the 16 species. We found no link between the intensity of competition experienced by the species and its shade tolerance.

We were able to analyse how intensity of competition varies with crowding at low or at high level of *WB* and *DD* simply by plotting the CRCs. This curve hardly varied in shape along bioclimatic gradients (Fig. 3); any variation that was found was generally smaller than the 95% credible intervals. The only significant variations highlighted that the effect of the stress varied with the crowding intensity; for instance the CRC of *Fagus sylvatica* increased with *DD* at a *CI* of 0.15, but decreased at a *CI* of 0.5, and the CRC of *P. abies* was unaffected by *DD* at a *CI* of 0.15 but increased at a *CI* of 0.5 (Fig. 3).

COMPETITION IMPORTANCE

Variation in competition importance along bioclimatic gradients was much stronger. For all species the importance of competition was greater at high values of *DD* or *WB,* where tree growth was most rapid (Fig. 4). The amplitude of variation exceeded the 95% credible intervals for most of the species (Fig. 4). However, the importance of competition was high (and the 95% credible intervals large) for some shade-intolerant species growing under xeric conditions (*Pinus sylvestris* and *Quercus robur*) and cold environments (*P. sylvestris*, *Pinus cembra*, *Pinus uncinata* and *Betula pubescens*). Also, the mean index of competition importance (computed over all the FNFI plots where the species was found) was much lower for shade-tolerant than shade-intolerant species (Fig. 5), and there was a significant negative correlation between the shade tolerance

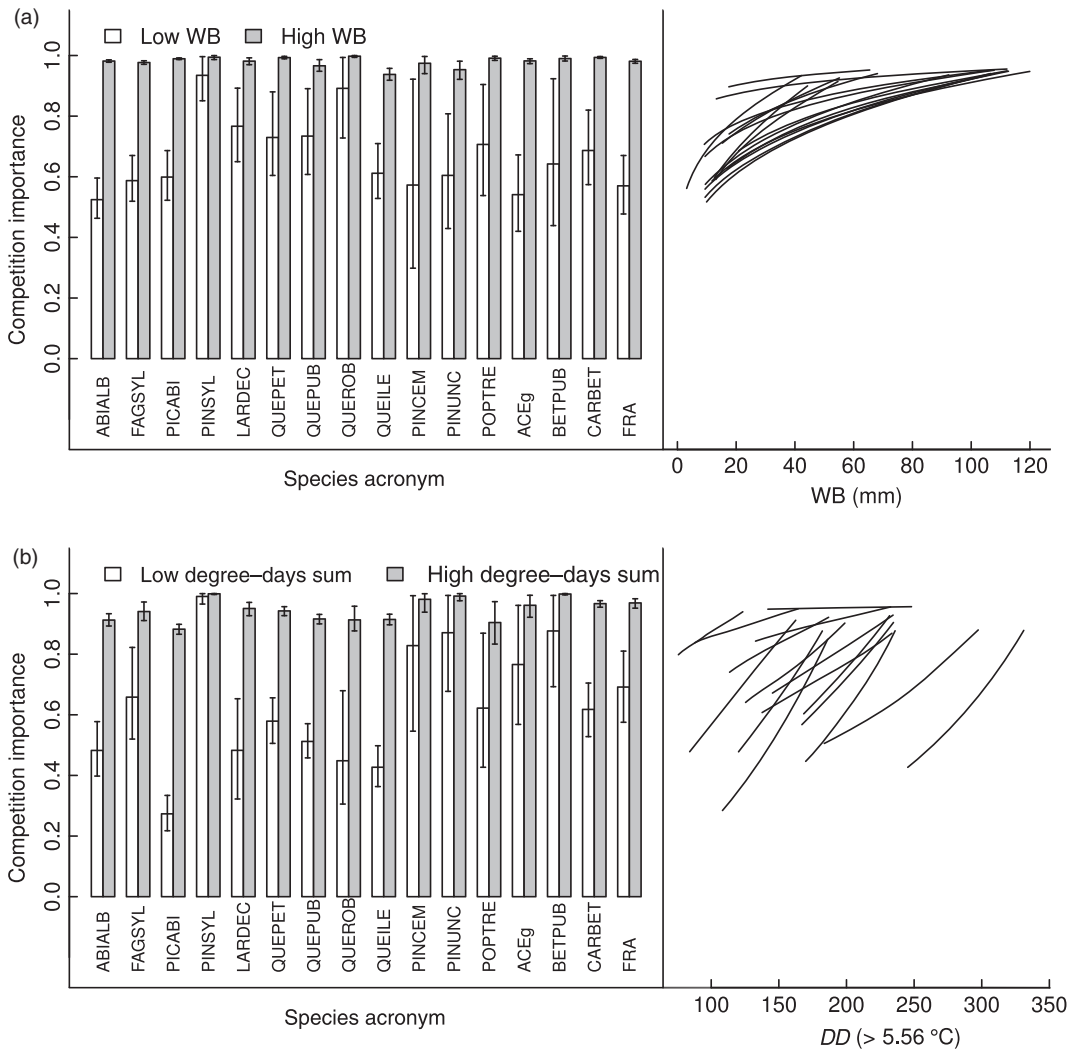

Fig. 4. Variation in competition importance between low and high value of (a) water budget (*WB*) and (b) degree-day sum (*DD*). The biotic interaction importance indices range from -1 (facilitation) to +1 (competition) and were computed at the 2.5% and at the 97.5% quantile of the abiotic condition experienced by the species (see text for more details). Non-overlapping 95% credible intervals (error bars) between high and low stress levels imply a statistically significant difference (at $P < 0.05$). The left panels represent the pattern of continues change of the index between high and low stress levels for the 16 species. See Table 1 for species acronyms.

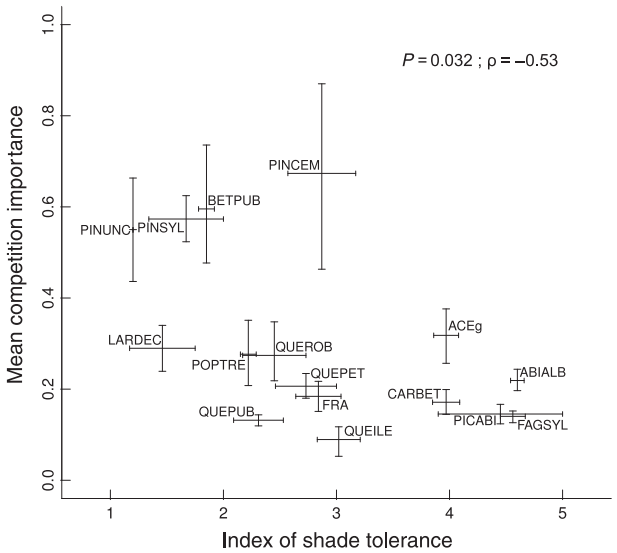

Fig. 5. Correlation between the mean importance of biotic interaction and shade tolerance indices for the 16 studied species. Indices of biotic interaction importance range from -1 (facilitation) to +1 (competition). Index of shade tolerance is based on Niinemets & Valladares (2006). Error bars represent the 95% credible intervals of the competition and shade tolerance index (when SD available in Niinemets & Valladares (2006)). Pearson's correlation coefficient and its *P*-value are given. See Table 1 for species acronyms.

index and mean competition importance ($\rho = -0.53$, $P = 0.032$). Note that *P. cembra* is classified as a rather shade-tolerant species by Niinemets & Valladares (2006) but has been considered as an intermediate shade-intolerant species by other authors (Rameau, Mansion & Dume 1993).

The effect of the *CI* on competition importance differed between species. All species reached an asymptote corresponding to maximum competition importance with increasing level of crowding both at low value off *DD* and at low value of *WB* (see Fig. S3). The response of shade-tolerant and shade-intolerant species differed. The shade-tolerant species (defined here as having an index above 2.5) presented much more significant variation of the importance of competition with crowding than shade-intolerant species. These differences were clear in the comparison of the competition importance at a *CI* of 0.02 and 0.7: for most of the shade-tolerant species these differences were greater than the 95% credible intervals, whereas for shade-intolerant species these differences were not significant (Figs 6 and 7). There were exceptions to this general rule among the shade-tolerant species, such as *Quercus ilex*, *P. cembra* and the *Acer* group for low *DD* conditions (Fig. 6) and *Quercus petraea, Q. ilex* and *P. cembra* for low *WB* conditions (Fig. 7). However, most of these exceptions were of medium shade tolerance (i.e. close to the threshold of 2.5). Overall, there was a significant correlation between the shade tolerance index and the magnitude of change of competition importance with *CI*, as indicated by the differences between the upper limits of the credible intervals at a *CI* of 0.02 and their lower limits at a *CI* of 0.7 (for *WB* $\rho = 0.56$, $P = 0.021$ and for *DD* $\rho = 0.59$, $P = 0.014$).

Discussion

INTENSITY OF COMPETITION VARIES LITTLE ALONG IMPORTANT BIOCLIMATIC GRADIENTS

The intensity of competition – in terms of its affect on adult growth – varied little in response to water budget (a resource) and degree-day sum (a non-resource). It was small in comparison to model uncertainty, even though growth varied profoundly along these bioclimatic gradients. In addition, none of the 16 species studied demonstrated a shift to facilitation according to the best-fitting model.

Few previous studies have analysed change in plant–plant interaction with abiotic stress for the adult tree stage. One study reported that neighbours facilitated the growth of mature trees in subalpine forest in the northern Rocky Mountains, probably through providing protection against blowing ice and snow (Callaway 1998). Coomes & Allen (2007) found no evidence of a shift to facilitation along an elevation gradient for adult *Nothofagus* trees in the New Zealand Alps. They even found that competition intensity varied inversely to the prediction of the SGH, with a slightly increased intensity at high elevation. Indirect analysis of adult tree competition based on spatial structure of tree communities also found no evidence in support of the SGH (Welden, Slauson & Ward 1988; Wilson 1991).

Our findings – based on the growth of adult trees – contrast with other research that focussed on herbaceous communities or small regenerating trees. Removal experiments in herbaceous communities often show that plant–plant interactions may shift from competitive to facilitative with increasing abiotic stress (Callaway *et al.* 2002; Holzapfel *et al.* 2006 and references in Lortie & Callaway 2006). Competition intensity either increases with increasing productivity (Kadmon 1995; Sammul *et al.* 2000; Zhang *et al.* 2008) or does not change detectably (Wilson & Tilman 1993; Cahill 1999; Gaucherand, Liancourt & Lavorel 2006). Experiments involving regenerating trees have produced similar findings (Kitzberger, Steinaker & Veblen 2000; Chambers 2001; Gómez-Aparicio *et al.* 2004). It may not be surprising to find no evidence of a shift to facilitation for adult trees as facilitation is generally thought to be more frequent at the juvenile stage (Callaway 1995). The patterns of change in intensity and type of plant–plant interaction may thus be different between herbaceous plants, the tree regeneration stage and the tree adult stage. Our results may reflect a lower sensitivity to variations in abiotic conditions and competition of trees at the adult stage than at the juvenile stage.

It is nevertheless important to underline that several limitations of our study may reduce its potential to detect a classic SGH response. Firstly, it is important to note that Goldberg & Novoplansky (1997) proposed that a decrease of competition intensity was most likely in terms of plant survival than plant growth – it could therefore be useful to extend our work to adult tree survival. Secondly, the FNFI data base covers a wide range of climatic conditions, but few plots are established near the tree line (only 34 plots above 2200 m a.s.l.) in the very harsh conditions where Callaway (1998) found a facilitative effect for adult trees. So it is possible that our

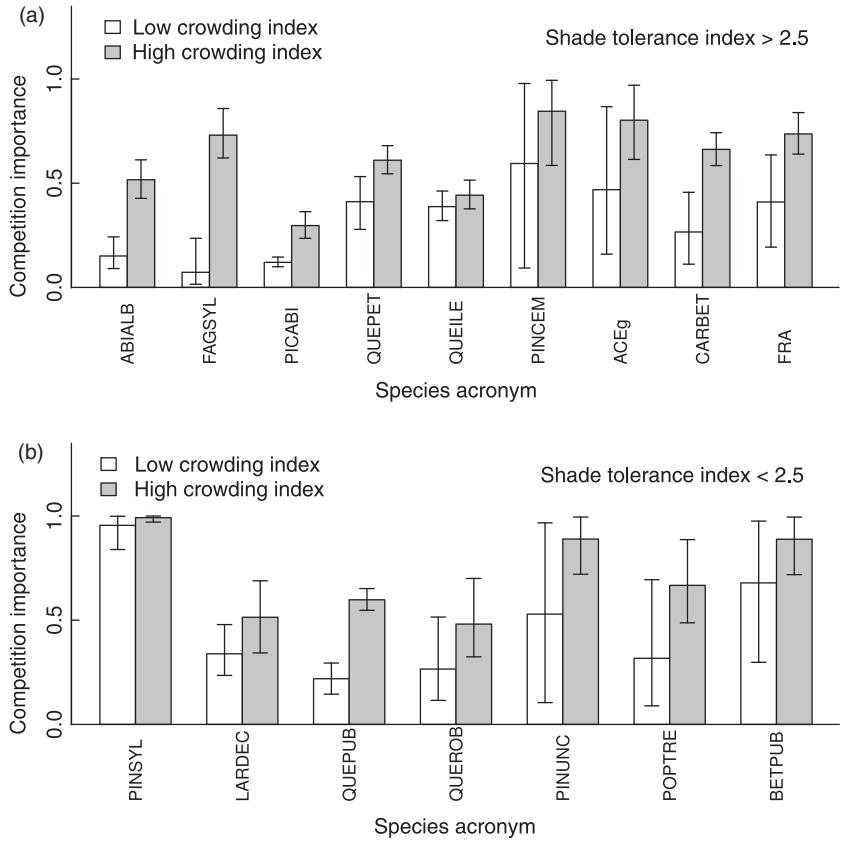

Fig. 6. Variation in competition importance between low and high crowding conditions (*CI* of 0.02 and 0.7, respectively) at low values of degree-day sum (*DD*) (high T° stress) for shade-tolerant and shade-intolerant species. The upper panel (a) shows the shade-tolerant species (shade tolerance index > 2.5) and the lower panel (b) shows the shade-intolerant species (index < 2.5). Low values of *DD* were determined as the 2.5% quantile of the abiotic condition experienced by the species. Non-overlapping 95% credible intervals (error bars) of the index between high and low crowding conditions imply a statistically significant difference (at $P < 0.05$). See Table 1 for species acronyms.

analyses miss out the extreme part of one of the abiotic gradients where the facilitative processes may be occurring. Nevertheless, our analyses have a large spatial and temporal scope and are thus well suited to detect dominant patterns in tree growth, supporting the idea that there is little variation in intensity and type of plant–plant interaction with increasing abiotic stress for adult tree growth.

IMPORTANCE OF COMPETITION FALLS WITH INCREASING ABIOTIC STRESS

The importance of competition – in terms of its affect on adult growth – increased with productivity along both bioclimatic gradients, i.e. fell with increasing abiotic stress. Previous experimental investigations in relation to the importance of competition have reported that it strongly decreases with increasing stress and that it does not necessarily correlate with competition intensity (Brooker *et al.* 2005; Gaucherand, Liancourt & Lavorel 2006). As has been the case for competition intensity, these studies have focused on herbaceous communities. The few studies on forest communities have been based on indirect approaches such as analysis of the spatial structure (Welden, Slauson & Ward 1988) or of the distribution of competition-related traits (e.g. maximum height) (Schamp & Aarssen 2009). These studies also reported a decrease of competition importance with increasing stress. Our study thus provides unique and compelling evidence, based on many tree species and over large environmental gradients, that the pattern of decreasing competition importance with increasing stress also holds for tree communities. It seems that this pattern is general and applicable to both herbaceous plants and adult trees.

Clear differences in the mean importance of competition appear between shade-tolerant and shade-intolerant species, with much higher importance values for shade-intolerant species. Given that competition for light is widely recognized as a major driver of forest community assembly and structure (Pacala *et al.* 1996), it is thus not surprising to see such differences between shade-tolerant and shade-intolerant species. For this reason the further development of a theory of plant–plant interactions along abiotic gradients should include plant strategies (Maestre *et al.* 2009), with shade tolerance being a trait of primary importance in the case of trees.

HARNESSING THE POWER OF NON-MANIPULATIVE APPROACHES FOR COMMUNITY-LEVEL RESEARCH

Our non-manipulative approach, using recent advances in Bayesian computational statistics, is complementary and not

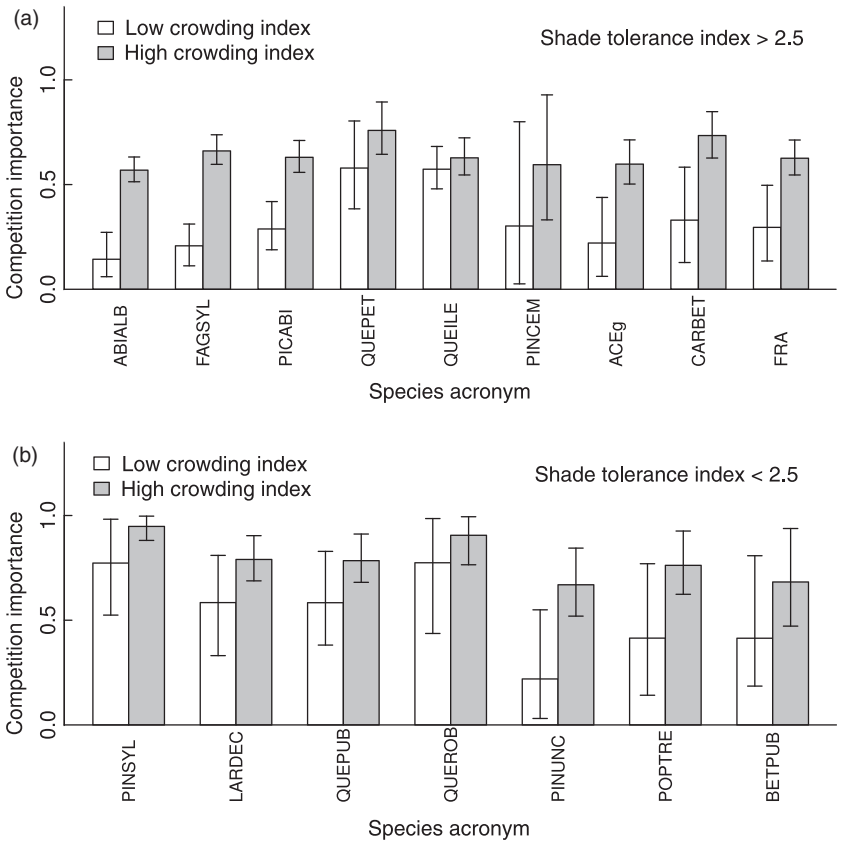

Fig. 7. Variation in competition importance between low and high crowding conditions (*CI* of 0.02 and 0.7, respectively) at low values of water budget (*WB*) (high water stress) for shade-tolerant and shade-intolerant species. The upper panel (a) shows the shade-tolerant species (shade tolerance index > 2.5) and the lower panel (b) shows the shade-intolerant species (index < 2.5). Low values of *WB* were determined as the 2.5% quantile of the abiotic condition experienced by the species. Non-overlapping 95% credible intervals (error bars) of the index between high and low crowding conditions imply a statistically significant difference (at $P < 0.05$). See Table 1 for species acronyms.

conflicting to traditional manipulative approaches examining plant–plant interactions (see Kikvidze & Brooker 2010 for a discussion about the merging of different approaches of competition importance). It allows us to harness the power of large data bases, such as national forest inventories, to analyse interactions between many species across their entire ranges using long-term response data (5-year growth averages). This sort of analysis is able to capture important processes driving the assembly and dynamics of forest communities. This advance should ultimately contribute to the development of a new theory of plant–plant interactions along bioclimatic stress gradients. One important difference between our approach and the traditional short-term removal experiment is that instead of simply comparing plants grown with and without competition, we can analyse plant–plant interactions through CRCs and how their shapes are affected by bioclimatic variables. These curves enabled us to identify important differences in the responses of different functional groups: for shade-intolerant species the competition importance is high even if they have only few neighbours, whereas for shade-tolerant species competition only becomes important at high crowding indices.

Ultimately the contribution of plant–plant interactions has to be evaluated on the structure and dynamics of communities (Freckleton, Watkinson & Rees 2009). Adult trees contain the majority of biomass of forests, are long-lived and have major influences on all other stages of the life cycle, thus quantifying the effects of competition on their growth is crucial. However, previous studies have concluded that even if competition intensity – in terms of its affect on plant growth – is high, it may not have an important effect on community structure (Lamb & Cahill 2008; Mitchell, Cahill & Hik 2009). Consequently, the effects of plant interactions on the community structure and composition cannot be fully understood simply by focussing on adult tree growth. The effects of these interactions on other components of the life cycle (such as seedling establishment and sapling growth and survival) must be quantified and integrated over the whole life cycle in a plant community dynamics model (Freckleton, Watkinson & Rees 2009) and be put in balance with the other factors important in structuring the community such as abiotic conditions, dispersal limitation, natural enemies, site history, and regional processes of speciation and extinction (Ricklefs 2008).

Our approach brings us a step closer towards community-level analysis of plant–plant interaction impact, because the growth predictions are easily integrated in individual-based models of forest dynamics such as SORTIE (Pacala *et al.* 1996; Clark *et al.* 2007; Kunstler, Coomes & Canham 2009). Such models could be used to understand how plant–plant

interactions drive plant community structure and dynamics. Nowadays many national forest inventory data sets are available, enabling researchers to test theoretical predictions about plant–plant interactions with non-manipulative estimations over unprecedentedly large spatio-temporal scales and species samples, and link such phenomenological competition models with models of community dynamics.

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Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Description of the water budget model.

Appendix S2. Likelihood of the model and prior description.

Table S1. Year of data collection and area for each *Département*.

Table S2. Parameter estimates of the growth model.

Figure S1. Effect of neighbourhood crowding on potential growth for three hypothetical species.

Figure S2. Growth response curves.

Figure S3. Variation in competition importance with crowding index at low values of WB and DD.

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